

HYDROPHILY: PHYLOGENETIC AND EVOLUTIONARY CONSIDERATIONS

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ABSTRACT

The two forms of abiotic pollination, hydrophily and anemophily, exhibit contrasting taxonomic, ecological and phylogenetic patterns. Anemophily is widespread among angiosperms whereas hydrophily occurs in only one dicot and seven monocot families. Ecological limitations of hydrophily likely parallel those of anemophily, yet the processes involved in the former are not well understood. Although hydrophily is in all probability polyphyletic, the phylogenetic relationships among hydrophilous groups are unresolved. Specialization in reproductive structures that accompany hydrophilous pollination makes the recognition of homology difficult, thus phylogenetic hypotheses in groups in which hydrophily occurs are tentative. Hydrophily and anemophily are both geographically widespread, yet the general trend of decreasing incidence of anemophily with decreasing latitude is lacking in the distribution of hydrophily. This contrast may be associated with markedly different geographic patterns of species richness in aquatic versus terrestrial habitats.

Key Words: hydrophily, species richness, geographic distribution, phylogeny, evolution

INTRODUCTION

Hydrophily, water-mediated cross-pollination, entails dramatic modifications of the floral systems of terrestrial angiosperms. These changes arise from adaptation to provide for the release, transport and capture of water-borne, often wet, pollen. Hydrophilous taxa are infrequent in angiosperms; only 140 of the total of ca. 225,000 angiosperms (R. Thorne, pers. comm.) are hydrophilous (.00062%). The infrequency of hydrophily has no doubt contributed to the perception that this pollination system is “unimportant” in angiosperm evolution. In fact, an understanding of hydrophily may provide a unique perspective on the evolution of angiosperm reproductive systems. Hydrophilous systems are perhaps the best examples of the evolutionary “plasticity” of the angiosperm floral biology; i.e., in hydrophily the “aerial” floral system that dominates angiosperms has been essentially abandoned. Furthermore, the restricted occurrence of hydrophily makes it possible to gain an overall understanding of its evolution, an

understanding which is perhaps unattainable in virtually all other, much more widespread pollination systems.

Two general, but sometimes rather arbitrary, forms of hydrophily are recognized: 1) epihydrophily; pollination via pollen transport at the water surface (two-dimensional), and 2) hypohydrophily; pollination via pollen transport below the water surface (three-dimensional). The distinctions between the two are not always clear and both may operate in some species. For the sake of discussion, the two are combined in this paper.

In most works on pollination biology, the two forms of abiotic pollination, anemophily and hydrophily, are treated conceptually as similar systems that operate in different media. There are no doubt similarities between anemophily and hydrophily that reflect their abiotic nature. However, it is evident that the two systems reflect contrasting ecological and evolutionary patterns. Several workers (e.g., Whitehead, 1969, 1986; Regal, 1983) have addressed the evolution of anemophily, especially in an ecogeographic context, but the evolution of hydrophily has been largely neglected. In fact, it may be informative to contrast these two abiotic pollination systems with the hope of elucidating the distinctions between them and to place these differences in an evolutionary context.

Many basic questions concerning the evolution of hydrophily remain unaddressed, or even unasked. For instance, although hydrophily characterizes all marine angiosperms, it is unclear whether it was a prerequisite for, or a consequence of, the invasion of the marine environment (Philbrick, 1988). Why is hydrophily most common in monocots, and virtually absent in dicots? What might this discrepancy suggest about the evolutionary histories of the monocots versus dicots? Are monocots, or certain groups within the monocots, somehow evolutionarily “predisposed” for hydrophily?

An enhanced understanding of the evolution of hydrophily may be attainable via consideration of the relationships among hydrophilous and nonhydrophilous taxa, the ecogeographic pattern of hydrophily, and its similarities and differences relative to anemophily. The purpose of this contribution is to consider these issues. First, our current understanding of the taxonomic and phylogenetic distribution of hydrophily will be summarized. Secondly, the ecogeographic distribution of hydrophily will be considered relative to anemophily, as well as several ecological and/

Table 1. The taxonomic distribution of hydrophily. Modified from Les (1988). The genera are followed by the number of species/type of hydrophily: E, epihydrophily; H, hypohydrophily. Taxonomy of monocots follows Dahlgren and Rasmussen (1983).

Dicot:	
Nymphaeales	
Ceratophyllaceae—cosmopolitan.	
<i>Ceratophyllum</i>	6/H
Monocot:	
Hydrocharitales	
Hydrocharitaceae—cosmopolitan, mainly warm regions.	
<i>Appertiella</i>	1/E
<i>Elodea</i>	5/E
<i>Enhalus</i>	1/H
<i>Halophila</i>	8/H
<i>Lagarosiphon</i>	9/E
<i>Nechamandra</i>	1/E
<i>Thalassia</i>	2/H
<i>Vallisneria</i>	2/E
Zosterales	
Najadaceae—cosmopolitan.	
<i>Najas</i>	30–50/H
Posidoniaceae—Mediterranean, S. W. Asia, Australia.	
<i>Posidonia</i>	3/H
Potamogetonaceae—(re: <i>Ruppia</i>) temperate and subtropical regions.	
<i>Ruppia</i>	1–7/E
Zosteraceae—temperate coasts, excluding South America and S.W. Africa.	
<i>Heterozostera</i>	1/H
<i>Phyllospadix</i>	5/H
<i>Zostera</i>	12/H
Zannichelliaceae—cosmopolitan.	
<i>Althenia</i>	2/E
<i>Lepilaena</i>	4/E
<i>Zannichellia</i>	1–5/H
Cymodoceaceae—tropical and subtropical.	
<i>Amphibolis</i>	2/H
<i>Cymodocea</i>	4/H
<i>Halodule</i>	6/H
<i>Syringodium</i>	2/H
<i>Thalassodendron</i>	2/H

or biological factors that may influence its distribution. Through a consideration of these two general topics I seek to focus attention on some of the important issues that remain to be adequately addressed regarding the evolution of hydrophily.

TAXONOMIC AND PHYLOGENETIC CONSIDERATIONS

The difference in taxonomic distribution of hydrophily in dicots versus monocots is striking. The Ceratophyllaceae is the single dicot family for which hydrophily has been documented. Although the Callitrichaceae is often cited as containing hydrophilous species, the available evidence suggests otherwise (Philbrick and Anderson, unpubl. data). In contrast, hydrophily is considerably more widespread in monocots, where it occurs in seven families (Table 1) and ca. 134 species (.0026% of monocots). If we consider the extent of hydrophily among aquatic angiosperms as a group, 1.5% of dicots, and ca. 28% of monocots are hydrophilous (Philbrick, 1990).

It has long been recognized that hydrophily has evolved several times. Yet, the taxonomic versus phylogenetic relationships are unclear; it is not evident how often it has evolved. In some instances, the taxonomic distribution of hydrophily, versus various manifestations of autogamy that have been misinterpreted as hydrophily, is still being clarified (cf. Philbrick, 1984, 1988). In addition, our understanding of the relationships among groups where hydrophily occurs is still tentative.

Hydrophily is likely monophyletic in dicots; it occurs only in the Ceratophyllaceae. Its phylogenetic history among monocots is much more complex. The seven monocot families in which hydrophily occurs are in two orders: Hydrocharitales and Zosteriales (Table 1). There has been much speculation concerning relationships among the families in these orders, yet study is plagued by the extreme modification of floral structure that masks homology. A recent cladistic analysis by Dahlgren and Rasmussen (1983) provided perhaps the best phylogenetic hypothesis of relationships among the families in these orders (Figure 1).

If we use the traditional idea that hydrophily arises from an aerial-flowered most recent ancestor, then the Dahlgren and Rasmussen phylogeny (Figure 1) suggested that hydrophily has evolved a minimum of four times in monocots: once in the Hydrocharitaceae (D), and at least three times in the Zosteriales clade (A, B, C). If we include the possibility of reversals from hydrophily to aerial pollination systems, several additional scenarios are possible. For instance, hydrophily may be synapomorphic at E in Figure 1, with a subsequent reversal to aerial pollination in *Potamogeton* (Potamogetonaceae) (Figure 1f). This latter “reversal-

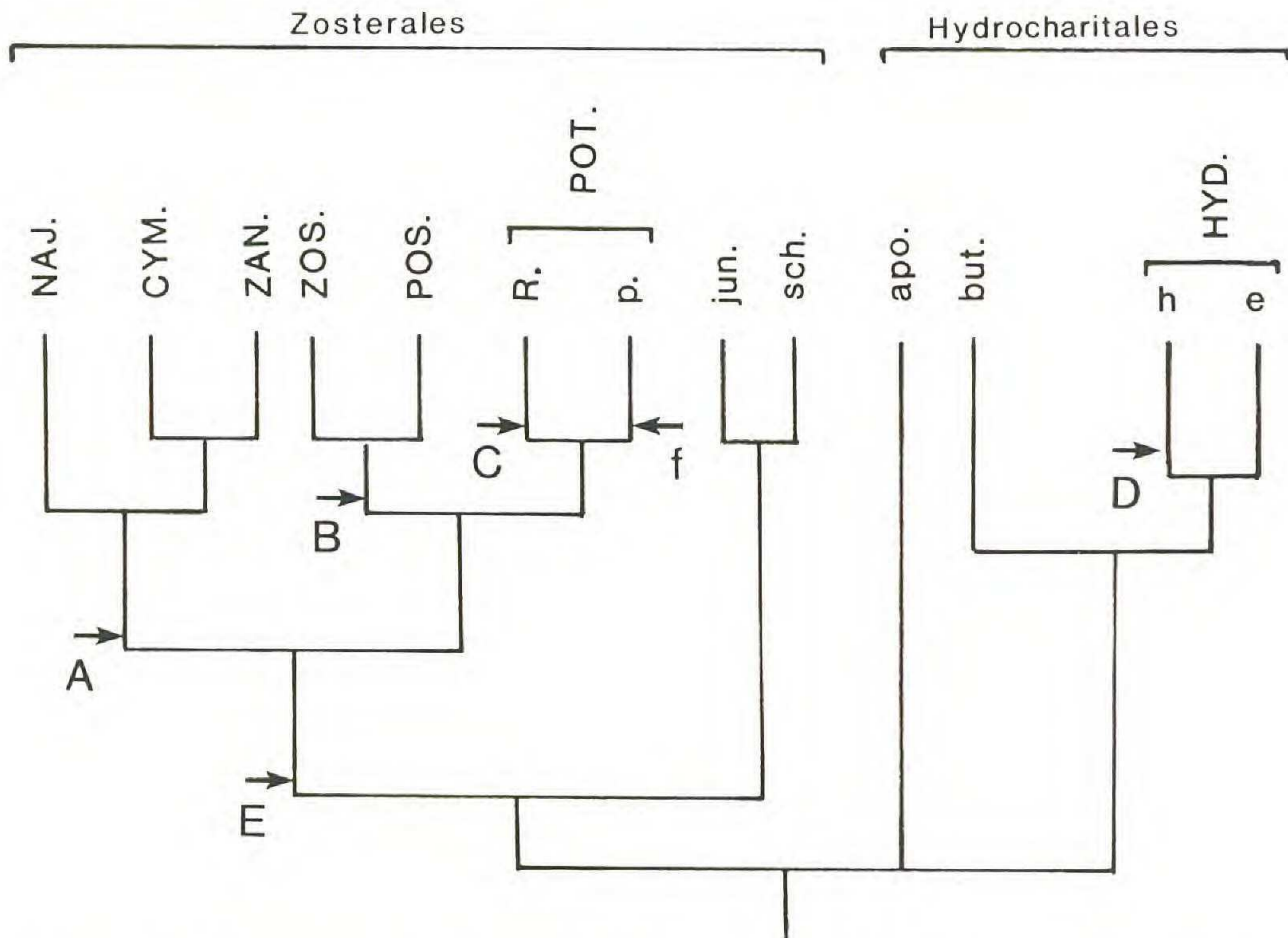


Figure 1. A cladogram modified from Dahlgren and Rasmussen (1983). The synapomorphies that support each node are not included but are listed in Dahlgren and Rasmussen's Figure 10, p. 359. Families in which hydrophily occurs are in upper case letters; those in which aerial pollination occurs are in lower case letters. The arbitrary division of the Hydrocharitaceae into hydrophilous (h) and entomophilous (e) taxa is mine. Upper case letters adjacent to arrows designate where hydrophily may have arisen; lower case letters adjacent to arrows designate reversals from hydrophily to aerial pollination systems. NAJ., Najadaceae; CYM., Cymodoceaceae; ZAN., Zanichelliaceae; ZOS., Zosteraceae; POS., Posidoniaceae; R., *Ruppia*; p., *Potamogeton*; jun., Juncaginaceae; sch., Scheuchzeriaceae; apo., Aponogetonaceae; but., Butomaceae; HYD., Hydrocharitaceae; POT, Potamogetonaceae.

scenario" requires one less step than does the former. However, the reversal-scenario requires the evolution of aerial pollination from a hydrophilous precursor, which is contrary to the traditional belief that aerial pollination systems are primitive. Yet, in principle there is no reason to refrain from reversing this polarity. Could aerial floral systems in some groups be derived from hydrophilous ones? At the species level there is no *a priori* reason why an aerial floral system cannot be derived from a hydrophilous precursor. In fact, it may be heuristic to consider just such alternatives, with the hope of gaining a new perspective on the problem. It is noteworthy that the resolution that involves the fewest

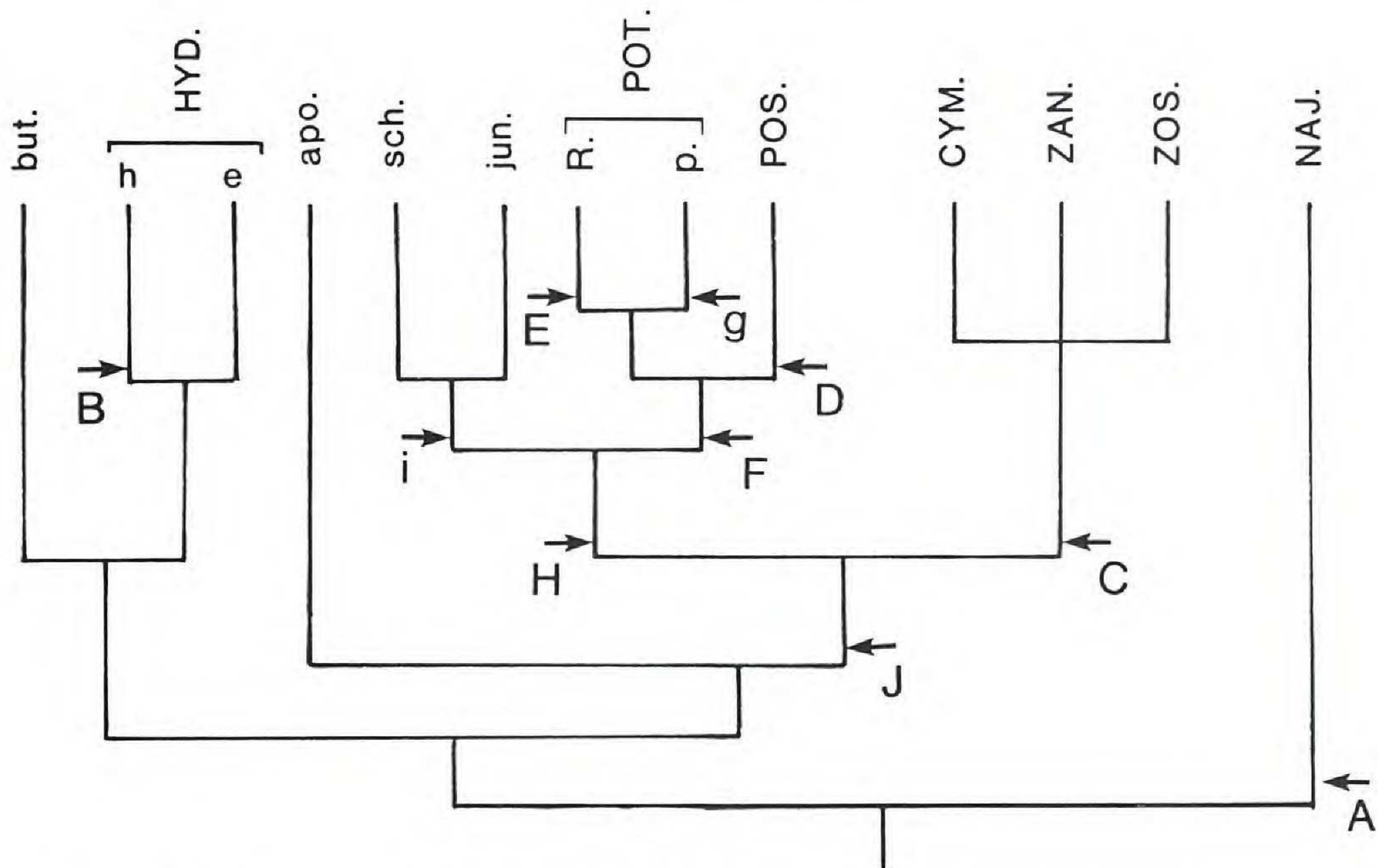


Figure 2. An intuitive phylogeny of Robert Thorne (pers. comm., 1990) illustrating the proposed relationships between the same families shown in Figure 1. Families in which hydrophily occurs are in upper case letters, those in which hydrophily does not occur are in lower case letters. For the sake of illustration the Hydrocharitaceae are arbitrarily divided into taxa that exhibit hydrophily (h) and those that are entomophilous (e). Upper case letters adjacent to arrows indicate where hydrophily may have originated; lower case letters represent reversals from hydrophily to aerial pollination systems. apo., Aponogetonaceae; sch., Scheuchzeriaceae; jun., Juncaginaceae; POT., Potamogetonaceae; R., *Ruppia*; p., *Potamogeton*; POS., Posidoniaceae; CYM., Cymodoceaceae; ZAN., Zanichelliaceae; ZOS., Zosteraceae; NAJ., Najadaceae; HYD., Hydrocharitaceae; but, Butomaceae.

steps (the reversal-scenario) includes a single reversal from hydrophily to aerial pollination.

It may be useful here to compare the cladogram from Dahlgren and Rasmussen with another phylogenetic pattern that has been proposed for the Zosterales. Figure 2 is the intuitive phylogenetic tree of Robert Thorne (pers. comm.). Several features of the Thorne phylogenetic tree contrast with that of Dahlgren and Rasmussen, e.g., Thorne's placement of the Najadaceae relative to the Zosteraceae. Using the same reasoning as above, the Thorne phylogenetic tree suggests that hydrophily has evolved at least five times in monocots (Figures 2A, B, C, D, E). If reversals to aerial pollination systems are included, the most parsimonious resolution would still require five steps. For instance, if hydrophily arose at A and B, to account for its occurrence in the Najadaceae

and Hydrocharitaceae, respectively, and at J, a minimum of two reversals (g, i) would be necessary. Thus, the Dahlgren and Rasmussen topology (Figure 1) provides a more parsimonious (fewer steps) resolution of the distribution of hydrophily than does the phylogenetic tree of Thorne (Figure 2).

The complexity of interpretation of floral structure throughout the Zosteriales has been an obstacle in establishing confidence in phylogenetic hypotheses for this order (Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983; Posluszny and Tomlinson, 1977; Tomlinson, 1982). This difficulty has been attributed to modification of reproductive structures that accompany the evolution of hydrophily. However, the presence of non-hydrophilous taxa in this order also leads to phylogenetic puzzles. Taxa such as *Lilaea* and *Triglochin* (Juncaginaceae) and *Scheuchzeria* (Scheuchzeriaceae) display floral features that are difficult to assess as homologous with those in other monocot groups (Tomlinson, 1982). Thus, it appears that there are factors other than hydrophily itself that make interpretation of phylogenetic relationship difficult in the Zosteriales. A reassessment of some of the basic ideas we have concerning floral system evolution, such as the evolutionary polarity of aerial versus hydrophilous pollination, may provide a new perspective.

It is important to note that neither the Dahlgren and Rasmussen (Figure 1) nor Thorne (Figure 2) phylogenies provide resolution for relationships among taxa in the Hydrocharitaceae (nor are they meant to). Yet, this family deserves special consideration here, given its diversity of pollination types. The Hydrocharitaceae is the only family in which entomophily, epihydrophily and hypohydrophily all occur (cf. Cook, 1982). Unfortunately, little phylogenetic work has been carried out in the Hydrocharitaceae (C. D. K. Cook, pers. comm.) and it is unclear whether hydrophily is mono- or polyphyletic in the family. Kaul (1968, 1970) included a diagram of floral evolution derived from his studies of floral and inflorescence anatomy. He showed that modifications of floral and inflorescence structures that accommodate hydrophily may have occurred via several developmental pathways. This evidence suggests that hydrophily is polyphyletic within the family. A phylogenetic framework against which to assess the evolution of pollination types would allow us to address whether one form of hydrophily has led to another (e.g., epihydrophily to hypohydrophily) or whether they have arisen independently.

TAXONOMIC, GEOGRAPHIC, LIMNOLOGICAL AND
BIOLOGICAL CONSIDERATIONS

Anemophily versus hydrophily: taxonomic distribution

The differences in taxonomic distribution of anemophily and hydrophily are striking. Anemophily is taxonomically widespread and occurs in virtually every major angiosperm group. Anemophilous groups are often species-rich; for instance, *Quercus* (Fagaceae) encompasses ca. 600 species, *Salix* (Salicaceae) ca. 400 species, and *Poa* (Poaceae) ca. 500 species. In addition, the Poaceae, a largely anemophilous family, has perhaps 6000 species. Thus, it is reasonable to say that speciation in these groups does not seem to have been hindered by an anemophilous pollination system.

Hydrophily, in contrast, is restricted to eight angiosperm families (Table 1). Groups that include hydrophily are generally species-poor (Les, 1988); in fact, *Najas* with its ca. 50 species is the most species-rich hydrophilous genus. The next largest hydrophilous genus is *Zostera* which has only 12 species. The remaining genera contain 10 or fewer species. Whether it is hydrophily itself or the associated attributes of life in the aquatic milieu which limit speciation is an issue which has been addressed to some degree by Les (1988), although it remains largely unresolved.

Geographic considerations

Although there are relatively few hydrophilous species, hydrophily itself is as geographically widespread as anemophily, yet the two abiotic pollination types show different geographic patterns. Anemophily increases in incidence with increasing latitude and/or altitude (Whitehead, 1969; Regal, 1983; Berry and Calvo, 1989). Anemophily is the primary mode of pollination across large geographic areas, e.g., northern boreal forests and grasslands. However, anemophily is relatively uncommon in tropical regions. In contrast, hydrophilous species seem to be equally common in temperate and tropical regions, but make up a small component of the flora throughout. All eight families in which hydrophily occurs are geographically widespread, and five of the eight families exhibit broad geographic ranges across temperate and many tropical regions (Table 1).

The broad distribution of hydrophily is illustrated by the num-

Table 2. Summary of the total number of species (A-C) and genera(D) that occur per 10 degrees of latitude. The taxa in each latitudinal increment are not necessarily mutually exclusive. A. The number of species of *Najas* in Central and North America (modified from Haynes, 1979). B. The number of species of *Najas* in the Neotropics (modified from Lowden, 1986). C. The number of species of *Najas* in Malaysia (modified from de Wilde, 1972). D. The number of genera of seagrasses worldwide (modified from den Hartog, 1970).

Degrees Latitude	<i>Najas</i>			Seagrasses
	A	B	C	D
70	—	—	—	2
60	2	—	—	2
50	5	—	—	4
40	7	4	—	6
30	5	4	—	8
20	5	5	4	8
10 N	—	5	3	8
0	—	5	7	8
10 S	—	3	—	8
20	—	4	—	11
30	—	2	—	8
40	—	—	—	2
50	—	—	—	—

ber of representative taxa that occur in temperate and tropical latitudes. For instance, Haynes (1979) and Lowden (1986) provided distribution data for species of *Najas* throughout Central and North America, and the Neotropics, respectively. The numbers of species of *Najas* per 10 degrees of latitude (Tables 2A, B) shows a relative overall geographic uniformity. The similar incidence of najad species in tropical and temperate regions contrasts markedly with what one would predict if the distribution of anemophily were used as a model: increasing incidence with increasing latitude. The distribution of *Najas* in Malaysia (de Wilde, 1972) also illustrates the extent of this genus in tropical regions (Table 2C). The temperate-tropical distribution of hydrophily is further illustrated by the worldwide distribution of the genera of sea-grasses (Table 2D). In fact, the number of genera per 10 degrees of latitude is somewhat higher in tropical than temperate regions.

The nature of the comparisons that are being attempted here lead to several questions. For instance, is this a meaningful comparison given the vastly different sample sizes? That is, there are

only 140 species of hydrophilous angiosperms, compared with the thousands of anemophilous taxa from which to assess distribution patterns. No doubt our perception of the distribution of hydrophily is colored by the distribution of relatively few species. However, this problem is inherent in the nature of the pattern being discussed, that is, comparing a ubiquitous to a rare pollination system. Secondly, although anemophily is infrequent in tropical regions relative to biotic pollination, how many tropical taxa are in fact anemophilous? Could it be that on a taxon-by-taxon basis anemophily is as frequent, or more frequent, in tropical regions as hydrophily? Although, this frequency comparison may or may not be true, the significance of the comparison being made lies in the incidence of the pollination system throughout broad geographic areas, not in its proportion relative to other pollination systems within a particular flora.

Limnological factors

Our understanding of hydrophily might benefit from a discussion of the factors that limit its distribution, an approach taken regarding anemophily (Whitehead, 1969; Regal, 1983; Daubenmire, 1972). The ecogeographic distribution of hydrophily is no doubt a result of a complex array of interactions of limnological and biological factors. Although we run the risk of over-simplification, it may be useful nonetheless to attempt to construct generalized patterns.

Aquatic habitats are considered fairly uniform regardless of latitude (Arber, 1920; Sculthorpe, 1967; den Hartog, 1970; Tiffney, 1981; Les, 1988). Although differences in water chemistry, growth season duration and temperature do affect aquatic plant communities, the aquatic habitat seems to be more uniform than terrestrial habitats, in part due to the thermal properties of water.

Environmental cues that initiate flowering in hydrophilous species may be insensitive to latitudinal change. The seagrasses (Cymodoceaceae, Hydrocharitaceae [*Enhalus*, *Thalassia*], Posidoniaceae, Zosteraceae) provide a good example, where tidal cycles have been implicated in stimulation of flowering (cf. Pettitt, 1984). Although the amplitude of the tidal cycle varies with latitude, the cycle itself is ubiquitous. Similar ubiquitous cues may also be instrumental in the flowering of freshwater hydrophilous taxa. However, pollination systems in freshwater hydrophilous

species are little studied. Therefore, possible environmental cues that would indicate the most appropriate environmental conditions for pollen release, transport, and capture have yet to be elucidated.

Nothing is known about the patterns of pollen flow (e.g., effective "pollen shadow," dispersal distance, etc.) relative to population structure, in hydrophilous species (cf. Les, 1988). The biotic and abiotic limits to pollen flow have not been identified. Nonetheless, some general assumptions are not unreasonable. An important component of the physical boundaries of aquatic habitats (the margins of the body of water) are insensitive to geography. That is, the physical boundaries to water-mediated pollen flow within a body of water will be the same regardless of latitude. This fact would certainly serve to "standardize" a major factor that limits pollen flow. Furthermore, the overall limnological processes that would influence pollen dispersal in water bodies of similar size would likely be the same in temperate and tropical regions. For instance, the yet poorly understood diurnal turnover of the water column in the littoral zone may provide a predictable vector for pollen flow within a population.

Biological factors

An important difference between aerial and underwater floral systems is the spectrum of potential pollen vectors: both biotic and abiotic (wind) vectors are available to aerial floral systems. In contrast, the aquatic medium itself is the only vector available to submerged flowers. Although a specialized fauna is well developed in aquatic plant communities, there is no evidence to suggest that biotically mediated pollination occurs in submerged flowering species. Thus, in underwater aquatic habitats, unlike in aerial systems, an increasing spectrum of biotic pollination vectors with decreasing latitude would have little bearing on the incidence of hydrophily. Some forms of epihydrophily (e.g., in *Elodea*, *Najas*, *Vallisneria*, Hydrocharitaceae) offer a different set of evolutionary riddles than does hypohydrophily. Many aspects of epihydrophilous pollination are essentially aerial in nature. Why epihydrophily is the method of pollen dispersal in some taxa of Hydrocharitaceae and anemophily or biotic pollination is not, is an intriguing yet unaddressed issue.

A consideration of species diversity in terrestrial versus aquatic

habitats is also revealing. It is generally agreed that species diversity is highest in the tropics and decreases with increasing latitude (e.g., Pianka, 1966 and references therein). For the angiosperms, this trend is based principally on terrestrial taxa. Although aquatic habitats in general display lower species diversity than their terrestrial counterparts, it is as yet unclear how aquatic plant communities vary latitudinally. A preliminary comparison of temperate and tropical aquatic habitats reveals that the species diversity of aquatic angiosperms in temperate regions is generally uniform with that found in the tropics (G. E. Crow, unpubl. data). Thus, the inverse relationship between species diversity and distance between individuals within a population, which serves to limit the effectiveness of anemophily (Daubenmire, 1972), is less a factor in aquatic communities. Cook (1988) reported that the incidence of anemophily in both temperate and tropical aquatic angiosperms was similar (ca. 33%). This observation too may suggest that species diversity in aquatic communities is similarly low in tropical and temperate regions.

But, how does this low diversity relate to abiotic pollination? Daubenmire (1972) proposed that the distance between individuals of a species restricts the effectiveness of anemophily; that is, the greater the distance the less effective is the pollination system. Furthermore, an inverse relationship exists between species diversity and distance between conspecifics. Thus, the high species diversity in tropical latitudes is strongly associated with the low incidence of anemophily in tropical regions. It is reasonable to assume that hydrophily is much like anemophily in that the distance between conspecifics is critical for effective pollination. Therefore, it is reasonable to predict that at a particular interplant distance, the effectiveness of hydrophily will also break down. Thus, the generally uniform distribution of hydrophilous species in temperate and tropical regions may reflect the relative uniform species diversity in aquatic habitats throughout both regions as well.

Assessment of the relative importance of seed set in the propagation of hydrophilous species is complicated by the high incidence of clonal growth. Les (1988) has discussed the apparent lack of genetic variability in many hydrophilous taxa and has suggested that in some groups sexual reproduction may be “essentially a relictual condition of uncertain consequence to their present reproductive biology.” The rather sporadic episodes of

flowering in some taxa supports this notion. However, when flowering does occur in these species, seed are produced. Thus the sexual apparatus, both structurally and functionally, is maintained.

Najas and *Zannichellia* are exceptional hydrophilous genera in being annual, and perhaps by necessity, exhibiting abundant seed production (Les, 1988). Both genera have as broad a geographic distribution as any of the clonal hydrophilous taxa (e.g., *Ceratophyllum*). The high seed set throughout the ranges of these genera provides strong evidence that hydrophily can also function throughout. Thus, sexual as well as clonal growth may both be important factors that provide for such broad geographic ranges of hydrophilous taxa. Perhaps the high incidence of clonal growth in aquatic taxa would also promote low conspecific distances within aquatic communities.

CONCLUSIONS

Hydrophily and anemophily present contrasting phylogenetic, biological and ecogeographic patterns. The broad systematic distribution of anemophily indicates a polyphyletic phylogenetic history. However, phylogenetic relationships among aquatic monocots are largely unresolved, and thus whether hydrophily is ancestral or derived in each group is unclear. If in each group hydrophily is derived, it may well have evolved as many as five times in monocots. Yet, if hydrophily is primitive in certain groups, relative to aerial (e.g., anemophilous) pollination systems, we will have to reassess the traditional perception of pollination system evolution. It is equally unclear whether hydrophily has evolved once or numerous times in the Hydrocharitaceae, a family that exhibits a remarkable range of pollination systems.

Because hydrophily and anemophily are both abiotic systems, many of the overall factors that limit their effectiveness are likely to be similar. However, different geographic patterns of species diversity between terrestrial and aquatic habitats may play a role in the contrasting geographic distributions of the two abiotic pollination systems.

Many of the mechanisms of water-mediated pollination are being reevaluated and ecological perspectives are becoming refined (e.g., Cox, 1988). However, a reliable phylogenetic base upon which to anchor our understanding of the ecological diver-

sity is yet lacking. Because the ability to assess homology between hydrophilous and non-hydrophilous groups is clouded by the degree of specialization and reduction in hydrophilous flowers, it is desirable to construct phylogenetic hypotheses via data sets that are divorced from the reproductive structures themselves; e.g., the use of molecular based data sets in hydrophilous groups is certainly an exciting prospect.

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